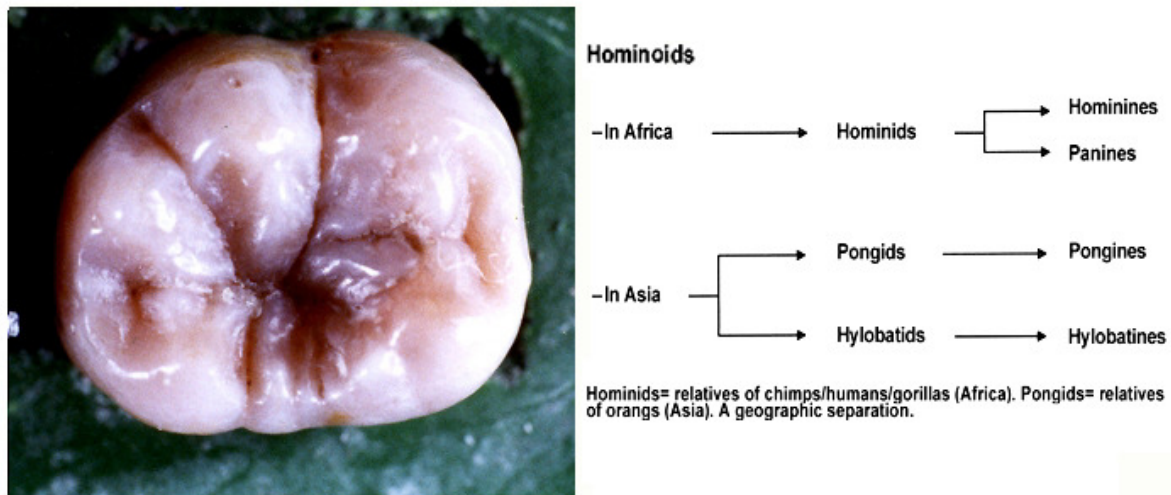


# ***Hominoid Phylogeny, the C/P3 complex and “Maxillary Canine Microwear in Dryopithecus From Spain”***

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## **Taxonomy and Evolutionary Relationships.**

Famous figures -as Lamarck or Darwin- have suggested a common ancestor to closely related species, as are the African great apes and humans. The Hominoid (apes and humans), forming a *super Family* bearing humanlike anatomical characteristics -e.g. having no tail, a relatively high and short skull and the 32 teeth of all the Old World simians with the lower first molar equipped with five cusps whose arrangement is shared with humans. The hominoid lineage became manifest in 1856 with the species *Dryopithecus* from tertiary territories. But, to-day, it is still difficult to ascertain if this great ape (~ 15 – 8 Ma old) belongs to pongids or to hominids.



The five-cusp and fissure pattern of the first lower molar teeth of *Dryopithecus*, known as the Y-5 arrangement, is typical of hominoids in general © P.-F. PUECH.

The simians have welded the mandible symphysis and mandible occlusion turned to be locked by the engagement of the canines. The projection of the upper canine (lacerative) requires a space (diastema) to fit in the opposite tooth row. Occlusion of upper canine with first lower premolar (C / P3) serves as a sharpener. We retain three functional domains to the C/P3 complex: mesioocclusal wear with the lower canine, tip wear, and distolingual wear facet with a third premolar (Puech P.-F. et al.1989 Maxillary canine microwear in *Dryopithecus* from Spain. Am. J. Phys. Anthropol.80:305-312). The oldest recovery of an “Ape” type locomotion has been found by S. Moyà Solà, not in Africa but in Catalonia in a 9.5 Myears old *Dryopithecus*.

In *Dryopithecus* the canine tip are blunt by puncture-crushing , with dentine more worn than enamel in the typical appearance of wear resulting from abrasion, as in gorilla, orang-utan, chimpanzee canines and in early hominids from Laetoli and Hadar (Puech and Albertini, 1984 Dental microwear and mechanisms in early hominid s from Laetoli and Hadar. Am. J. Phys. Anthropol. 65:87-91). Wolpff M.H. reported in PaleoAnthropology (2006: 36-50) that to

varying extents, a number of Miocene ape canines evince a canine tip with a similar pattern. The C/P3 complex of our closest ancestors tells a series of events concerning human origins: changes in canine crown shape and reduction of the longest dimension within the hominine clade have eliminated the honing upper canine / lower premolar P3 occlusal specialization of apes. Decrease of the maxillary canine projection has given more occlusal leeway and transformed the dental occlusion function of hominines. Premolars P3 tend to become more molarised providing evidence for the changing biological role of this tooth. The result is that mandibular premolar heteromorphy (P3 compared to P4) is minimal in later hominines, including *Homo sapiens*.



*Gigantopithecus* (mandible 1) in occlusal (image reversed) and lateral views, showing the teeth between the first molar and the lateral incisor. The canine wear is similar to that of other Miocene hominoids. Note that the top of the mandibular canine is worn flat, and the distal edge is transversely worn. This wear results from edge-to-edge occlusion and puncture crushing © Milford H. Wolpoff.

The morphological evidence used to define humans is reinforced after the divergence from the apes that was carried out 8-7 million years ago. Australopithecines, which have an antiquity of ~ 5 Ma, were bipeds and that is the reason why *Homo* and *Australopithecus* are grouped as “hominines”. But the African apes’ knuckle-walk may have evolved from some kind of bipedal locomotion shared by the hominines ancestors (Verhaegen M. and Puech P.-F. 2000 Hominid lifestyle and diet reconsidered and comparative data. *Hum. Evol.* 15: 151-162).



## Maxillary Canine Microwear in *Dryopithecus* From Spain

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**KEY WORDS** *Dryopithecus*, Canine, Tooth-wear, Diet

**ABSTRACT** The three functional domains of the upper canines of *Dryopithecus* from Spain are analysed through microscopic examination. Evidence is presented that shows a food choice in concordance with open woodland habitat.

The hominoid lineage that leads to man first emerged in 1856 with the species *Dryopithecus fontani* recovered from tertiary territories of Saint-Gaudens, France (Lartet, 1856). In 1913 Luois Mariano Vidal reported the recovery from Cataluna (Spain) of a mandible of an animal belonging to the same species. Since then several other finds of *Dryopithecus* have been made from St. Quirze, Castell de Barbera, Can Ponsic, Can Llobateres, Can Gabarro (Polinya II), La Traumba (Viladecavales), Hostalets (Can Vila), Hostalets (Can Mata I), and El Firal by investigations supported by the Catalan Institute of Palaeontology from Sabadell (IPS).

*Dryopithecus* shares a set of derived characteristics with living great apes and humans, for example, robust canines and premolars (Andrews, 1978). Some features also distinguish the species of *Dryopithecus* between localities; for instance, tooth specimens from France, Germany, Austria and Hungary are characterized by relatively smaller, peripheralized, sharp molar cusps and Spanish samples by more rounded cusps, shallow mandibular corpora, and broad extramolar sulci (Begun, 1988). Because Spanish dryopithecines are probably from subtropical open habitats (Nagatoshii, 1987), they may have been adapted to a habitat that is generally drier than that of Central Europe at the same time. As a result, they may exhibit dental microwear patterns indicative of a different diet as compared with the dryopithecines of Central Europe.

Variations in maxillary canine microwear can be related to variations in canine form and function, through the identification and analysis of different wear facets on the ca-

nine. Thus, microwear analyses of dryopithecine canines should lead to insights into both canine use and microwear formation.

### MATERIALS AND METHODS

Dental microwear was observed on canines from the deposit of Can Llobateres (near Barcelona, Spain), the type of stratum site of the Vallesian. The Vallesian has an ecological character intermediate between "forested" and "savanna" biotypes (Crusafont-Pairo and Golpe-Posse, 1973). Thirty-three pongid specimens were found at Can Llobateres, where Hipparion remains are also abundant (Bernor, 1983). The faunal list appears in Crusafont-Pairo and Golpe-Posse (1973).

Four pongid species have been described from Can Llobateres: *Hispanopithecus laietanus*, *Dryopithecus piveteaui*, *Rohanapithecus sabadellensis*, and *Dryopithecus* cf. *indicus*. Dryopithecine canines found in the Can Llobateres deposits vary from a relatively gracile to a more robust tooth with a predominant mesiolingual furrow. Three primate canines were examined in the present study. Based on size and morphology, two canines were from females and one from a male. The male canine, ISP 41 (Fig. 1), is referred to *D. indicus* due to analogies with Chinji 13857 and Nagri 19057 of the Siwaliks (North India), but it is also very similar to *D. nyanzae* of the Mio-Pliocene transition Fort Ternan 20899, Kenya (Crusafont and Golpe-Posse, 1973). The crown IPS 41 is the most massive of all the Can Llobateres ca-

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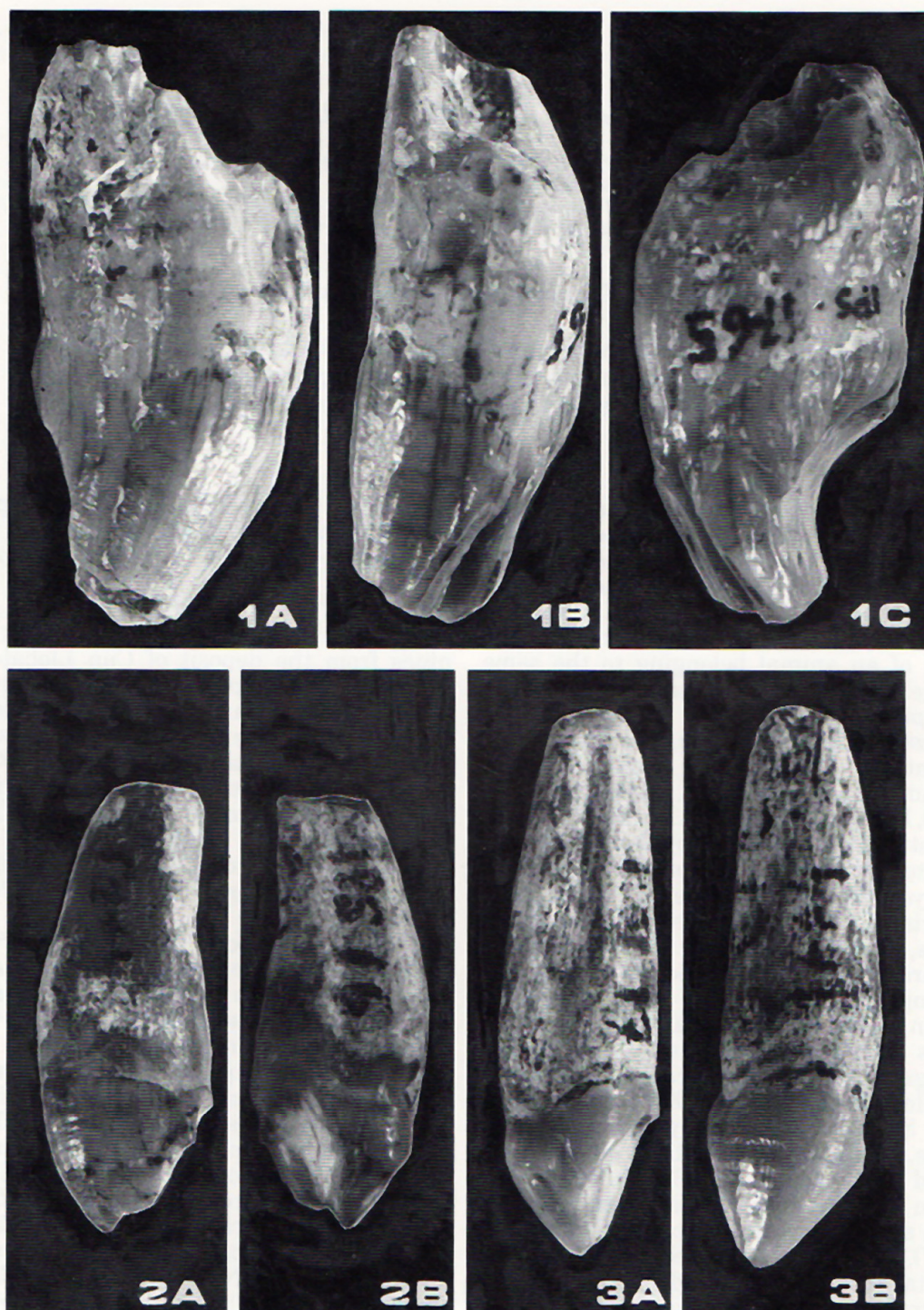


Fig. 1. IPS 41 right upper canine. A: Distobuccal; B: Mesiobuccal; and C: Mesiolingual views.

Fig. 2. Left upper canine ISP 16. A: Buccal; and B: Lingual views.

Fig. 3. Right upper canine ISP 17. A: Lingual; and B: Buccal views.



nines, with its anteroposterior length of 14.5 mm and width of 11.1 mm; this nearly equals the large Fort Ternan male KNM FT 39 assigned to *D. nyanzae* (Andrews, 1987) and reassigned to *Kenyapithecus wickeri* (Pickford, 1985). The crown bears a mesiolingual deep groove that extends vertically from the tip onto the cervical line, turning into a furrow at the root level. The ridges bordering this modified anterior lingual fovea, in addition to honing the lower canine, may serve to maximize occlusal pressure in limiting the area of contact (Zingesser, 1969). The female upper canines examined, ISP 16 and ISP 17 (Figs. 2, 3), have a much less pronounced mesiolingual groove than IPS 41. In all pongid species, this groove is pronounced in males and barely discernible to many females (Kelley, 1986).

The specimens were carefully cleaned with acetone. Then a nitrocellular impression was made with varnish, yielding a negative copy of the surface that was easily examinable by scanning electron microscopy (SEM) or by photonic transmitted light. Negative impression provides more details and less artifacts than duplication with a two-step replication (Unrath and Lindelmann, 1982–1983). Wear traces were observed under magnifications from 50 to 3,000 using the techniques described by Pfefferkorn and Boyde (1974).

#### RESULTS

As the occlusal relationships and functions of the maxillary canine in hominoids is well known, the present study examines the three functional domains separated by Zingesser (1969): mesioocclusal wear with the lower canine, tip wear, and distolingual wear facet with a third lower premolar.

The original piercing function of ISP 16, 17, and 41 has been partly lost through wear, as the crowns of these teeth are missing the sharp cusp tips. In ISP 41, part of the tip evidently was broken during life, and the remainder blunted by wear. There is a small V-shaped worn depression in the tip. The highly polished surface, photographed under SEM suggests that puncturing and high-pressure crushing has worn down the surface. This has led to a fatigue type of wear, as evidenced by the large pits and pebbly texture (Fig. 4) visible on this wear surface (Rensberger, 1978). There is no evidence that the tip had direct contact with an opposing tooth because the enamel edges are

blunt, and dentine is more worn than enamel in the typical appearance of wear resulting from abrasion (Hiiemae and Kay, 1973). On the tip of ISP 16, tooth/food/tooth contacts have produced very small elongated striae with many superimposed pits and raised boundaries of enamel prisms oriented parallel to the surface in the Hunter-Schreger bands (Figs. 5, 6).

In pongids and Laetoli-Hadar fossils, the distolingual surface of the upper canine (C') wears against the mesiobuccal surface of the lower third premolar (P3). The thin lingual plate of enamel of C' is quickly removed, exposing dentin and leaving a hard and sharp labial rim of enamel on the distal edge. Examined by SEM, this facet, the result of a tooth/tooth wear in a honing mechanism (Walker, 1984) reveals series of ridges and minute parallel scratches (Fig. 7). On the lingual area, out of the honing facet, there are only parallel scratches and no ridges, as there was no surface direct contact with the opposite tooth, and the wear was due to tooth/food/tooth action (Fig. 8).

The situation of the P3 facet is very similar to the opposing distolingual C' facet (Fig. 9). As a result of slicing action and self-sharpening, these surfaces have developed an indented angle that can also be observed on the mesial facet of the C' in the place where this tooth comes into tooth/tooth contact with the lower canine (Fig. 10). Sharp-edged facets have to be self-sharpening. This occurs by enamel being worn by enamel particles probably produced by adhesive and fatigue wear in a honing mechanism as described by Zingesser (1969). The mesial wear facet of ISP 41, caused by contact with the distal surface of the mandibular canine, is divided by the characteristic deep groove already mentioned in the description of the material. Microwear analysis reveals the relationship between this morphology and function. The enamel edges are pitted and scratched, whereas the dentine is only scratched. This indicates that the jaw movements producing the wear were mainly vertical closing movements on enamel edges, coupled with slight lateral excursions on dentin. Along the enamel edge, subparallel striations are visible within regularly spaced crenulations 0.2 mm apart (Fig. 12). These ridges, which are associated with changes in enamel prism direction, are called *Hunter-Schreger bands*. They are shallow, because tooth/tooth contact removes any relief. Dentine hollowing usually occurs along trailing enamel edges



and thus can be used as an indicator of jaw movements (Greaves, 1973). In the present case, adjacent dentine is less scratched than enamel and is not hollowed, as is usually the case, due to its lesser resistance (Fig. 13). Thus, foods have been cut only by leading enamel edges when opposed tooth surfaces came to move parallel to each other (Kay and Hiiemae, 1974).

On the trailing portions of the serrated enamel and dentine surfaces of the mesial wear facet, we infer a greater predominance of abrasion (tooth/food/tooth contact) over attrition (tooth/tooth contact). During mastication, food is present, in different degrees, between the surfaces of the occluding teeth. Still the occlusal surface can be divided into occlusal contact areas (OCA), where tooth/tooth contacts occur, and contact-free areas (CFA), where abrasive wear predominates. Enamel in OCA is worn into a nearly flat plane covered by some scratches, as few abrasive food particles are always present (Teaford and Walker, 1983). In CFA a fine abrasive action produces differential wear rates of the enamel structures that are not immediately obliterated by direct tooth/tooth contact (Fig. 14). Differential wear caused by changes in enamel prism direction in Hunter-Schreger bands can be associated with numerous microscopic striations caused by coarse abrasion (Fig. 15).

#### DISCUSSION AND CONCLUSION

Experimental results noted by Peters (1982) indicate that puncture-crushing usually does not produce microscratches unless food is covered with grit. Puncture-crushing generally leads to cusp tip blunting (Hiiemae and Kay, 1973) and differential wear of enamel, and dentine exposed on the cusp tip can be observed in the premolar and molar teeth of the Spanish dryopithecines (Figs. 16, 17). This action is associated with blunted cusps as in gorilla, orang, and chimpanzee canines (St. Hoyer and Koritzer,

1971) and in early hominids from Laetoli and Hadar (Puech and Albertini, 1984). Numerous vertical microscopic striation on the buccal enamel surface of the canine (Fig. 18) confirm the puncture action of the upper canine as a result of "insertion" into food material.

The postcanine teeth also exhibit polished and pitted occlusal enamel surfaces with random scratch distribution (Figs. 16, 17). This suggests a crushing function without direct contact guidance of the opposite teeth, which again implies a diet including hard material. Perhaps a puncture action was used to crack open food items of combined texture, e.g., nuts and seeds (Chivers et al., 1984; Kay and Hiiemae, 1974; Osborn and Lumsden, 1978; Rensberger, 1978).

In animals that consume seeds from acidic ripe and unripe fruits, SEM analyses have detected a more intensive erosive action on dental tissues than in other omnivores (Puech, 1986). Thus, the slight erosion of enamel surfaces observed in dryopithecines from Spain (Fig. 19) may be the result of food choice. It may also be of postmortem origin as suggested by Teaford for *Homo habilis* (1988); however, SEM chemical analysis has detected tooth surface deposits of alkaline pH carbonates such as gypsum (Fig. 20). As these substances are immediately soluble in acid, their presence on the teeth suggests the impossibility of postmortem acidic degradation after burial.

Finally, if food acquisition by pongids must be studied with their habitat, pitted occlusal enamel surfaces in canines and postcanine teeth may be related to the suggested environmental changes during the Miocene of Spain, from forested to more open woodland habitats. This would explain the anatomical features, such as rounded tooth cusps found in the Spanish dryopithecines, that maximize the permissible occlusal pressure without breakage. The Spanish dryopithecines may have been adapted to the

Fig. 4. ISP 41: pebbly texture on dentine of the tip and tubule structure.  $\times 1,000$ .

Fig. 5. ISP 16: blunt enamel of the tip with Hunter-Schreger bands.  $\times 120$ .

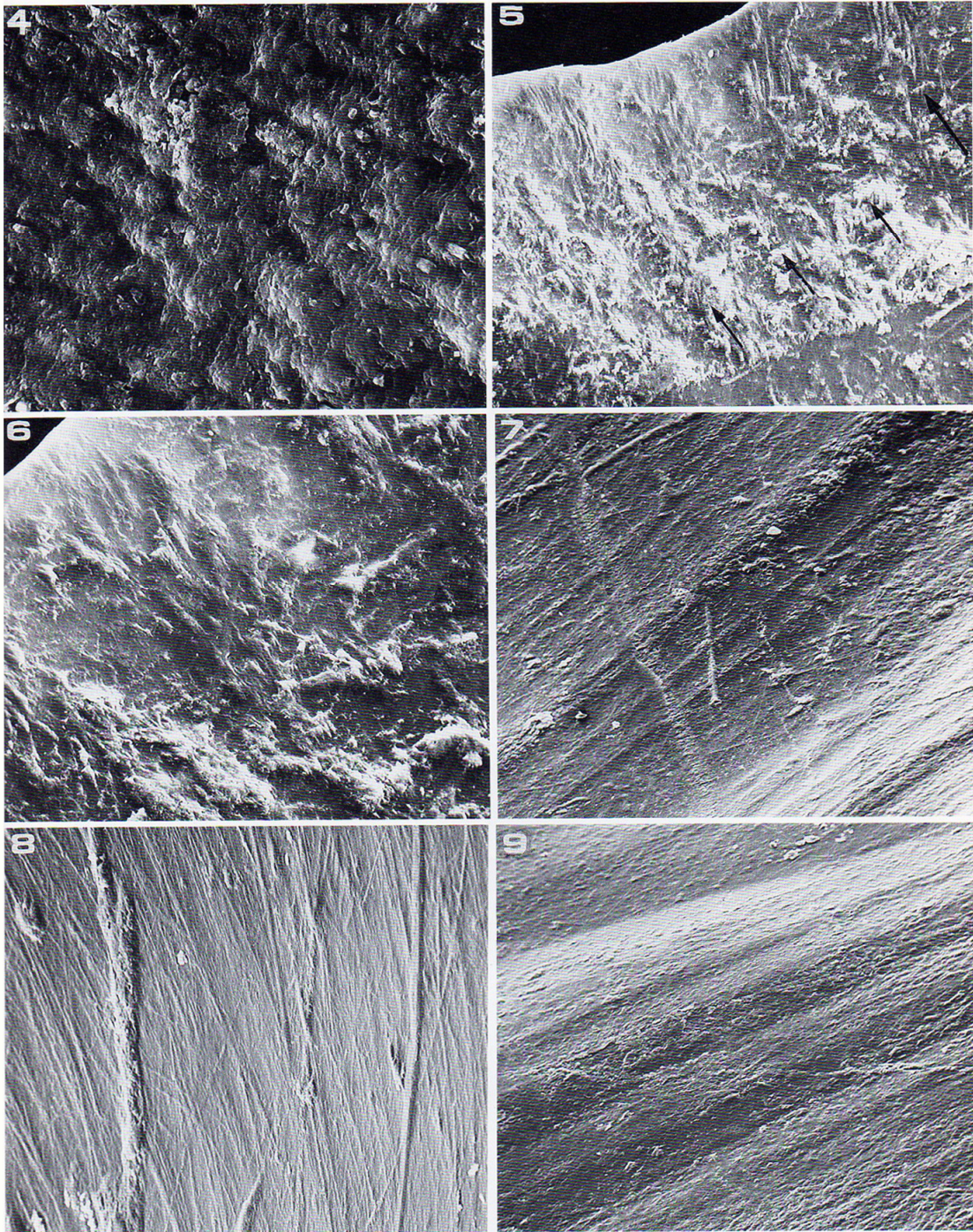
Fig. 6. ISP 16: higher magnification. No secondary alteration has erased the enamel structure revealed by the breakup of surface by microchipping.  $\times 300$ .

Fig. 7. ISP 41: honing distolingual wear facet of C' (enamel at top). Tooth-on-tooth wear.  $\times 100$ .

Fig. 8. ISP 16: abrasive wear on the lingual surface.  $\times 200$ .

Fig. 9. ISP 7: honing facet of P3 very similar to the opposed C' facet.  $\times 80$ .







consumption of woody vegetation rather than grasses.

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Fig. 10. ISP 16: tooth-on-tooth edge wear of the mesial facet of C' produced with the lower canine in a slicing action.  $\times 120$ .

Fig. 11. ISP 41: mesial wear surface, enamel edge at right and dentine abrasion on center left side with striations giving evidence of the direction of jaw closure.  $\times 50$ .

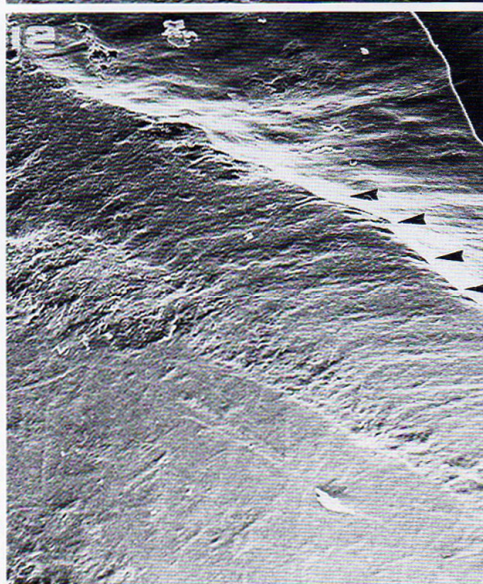
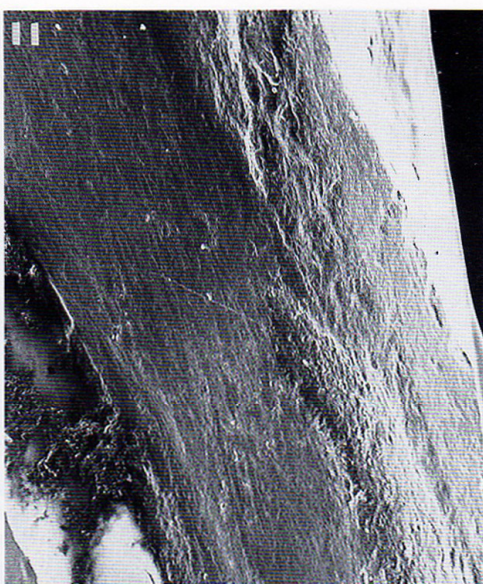
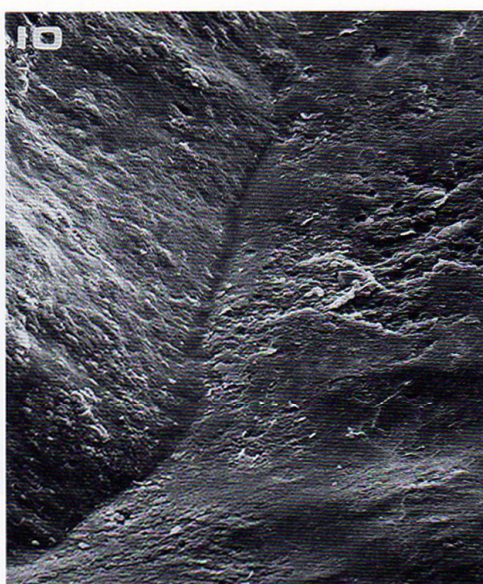
Fig. 12. ISP 41: shearing action of the enamel edge of the mesial surface with crenulations regularly spaced 0.2 mm apart. Dentine wear, lower right side, gives evidence of a crushing action.  $\times 50$ .

Fig. 13. ISP 41: a closer view of Fig. 12 at enamel-dentine junction indicates that enamel chips produced by attrition have not been trapped by dentine, at top, as no continuity in scratches is evident.  $\times 75$ .

Fig. 14. ISP 17: on the trailing portions of the serrated enamel of the mesial wear surface, we can differentiate abrasion in contact-free areas from attrition in occlusal contact areas. Crenulations are very deep in contact-free areas.  $\times 75$ .

Fig. 15. ISP 17: differential enamel and dentine wear in a trailing portion of the mesial wear surface.  $\times 75$ .







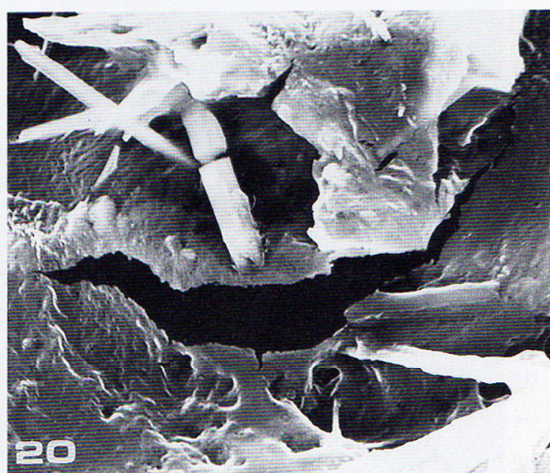
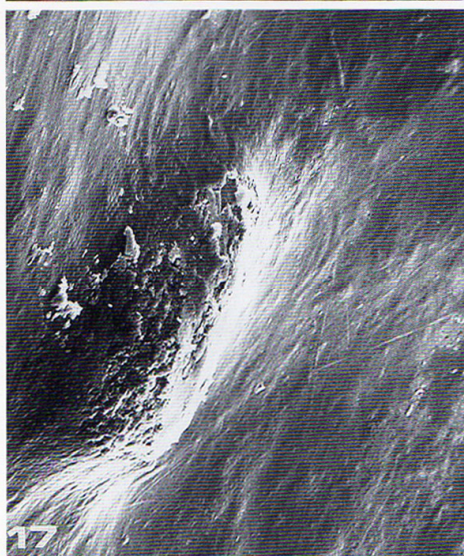
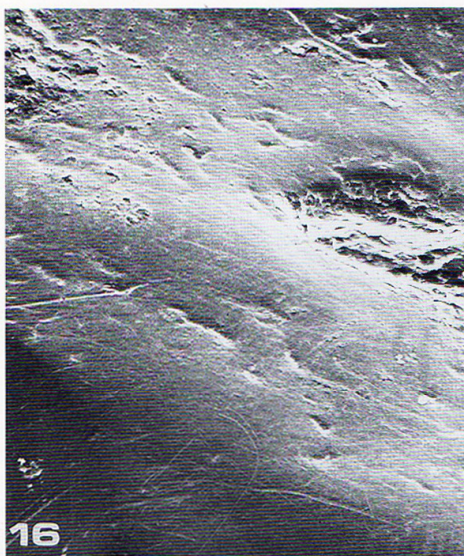


Fig. 16. ISP 7: puncture-crushing action on the cusp tip of right lower P4. The degree of enamel pitting is assumed to vary with the crushing activity.  $\times 150$ .

Fig. 17. ISP 1: dentine exposed on the cusp tips of the right lower 2nd molar. Striae are dominant on the leading edge of the enamel marginal ridge of dentine exposure.  $\times 130$ .

Fig. 18. ISP 16: wearing of the buccal surface of canine by "insertion" gives vertical striae normal to perikemata.  $\times 200$ .

Fig. 19. ISP 70: acidic food is evidenced by characteristic features such as pattern of furrows on enamel near dentine exposure in contact free areas.  $\times 300$ .

Fig. 20. gypsum tooth surface deposits on ISP 16 dentine.  $\times 3,000$ .